Criteria for Categorizing Feeding Types in Bivalves

BY

ROBERT G. B. REID

Department of Biology, University of Victoria, Victoria, British Columbia, Canada

THE PROBLEM OF SUBDIVIDING groups of organisms according to criteria other than phylogenetic relationships necessarily involves arbitrary divisions. This is so for categories of feeding types in the bivalves, and as POHLO (1969) points out confusion ensues if the arbitrary criteria are ill-chosen.

If a bivalve feeds on suspended particles it is called a suspension feeder, whether the particles are planktonic in origin, or are stirred-up deposit particles, and if a bivalve orientates its siphon to take up material at or near the surface of the substrate it is called a deposit feeder, although it may take up suspended particles also. Since both types of food are likely to be ingested at some time or another is the distinction worth perpetuating?

Both Pohlo and myself (REID & REID, 1969) use the behaviour of the inhalant siphon as the chief criterion for classification of feeding types, but I believe that this matter deserves a more exhaustive consideration. The feeding of a bivalve involves several stages: 1. siphon behaviour, which can determine the uptake of suspended material, deposited material, or both; 2. pallial sorting activities, which can reject the majority of particles drawn in through the inhalant siphon; 3. gastric processes which may reject particles on the basis of size, density or indigestibility. If categorization is to be based on a single criterion it should be the type of food from which the animal derives the bulk of its nutritional requirements. However, all three feeding stages deserve attention.

There are three possible food sources for these molluscan microphages: phytoplankton, detritus, and the microflora and microfauna found growing on the surfaces, and in the fissures of organic and inorganic particles. Since bivalves are unable to distinguish between detritus and its associated microorganisms this leaves us with only two categories: those animals which depend mainly on phytoplankton, and those which depend mainly on deposit materials and their associated microorganisms. These two categories correspond with what have been called in the past suspension feeders and deposit feeders respectively. However, in our work on the genus *Macoma* (REID & DUNNILL, 1969; REID & REID, 1969), which seems to run the whole gamut of feeding behaviour and food sources found in the Tellinacea, we further divided the deposit feeders into two categories: those which ingest fine deposits only, and those which ingest sand grains and presumably derive their food from the microorganisms associated with the sand grains. Finding an apt name for the latter category has so far eluded me. The feeding characteristics of these three groups are as follows:

Suspension Feeders – siphons project from the substrate; pallial sorting mechanisms accept particles up to 100μ; stomach contents characteristically green or brown from the preponderance of phytoplankton, though in winter months are colourless and have same constituents as the deposit feeders.

Fine Deposit Feeders – siphons lie along the surface of the substrate and the tip of the inhalant siphon may bend over to touch the surface and take up clumps of deposit material; pallial sorting mechanisms reject most particles more than 20μ; stomach contents are mainly small particles of organic debris and silt, together with small phytoplankton.

Sand Grain Feeders – inhalant siphon describes circles, with the tip touching the substrate and taking up sand grains and deposit material; pallial sorting mechanisms accept particles up to 300μ and more; stomach contents are mainly large sand grains, together with phytoplankton; stomach has large embayment protected by an extension of the crystalline style; gastric esterases and proteases are stronger than in the other two groups (REID & DUNNILL, 1969, and unpublished work).

NOTES

1. I use the expression "pallial sorting mechanisms" in the broad sense, since in our work on *Macoma* (REID & REID, 1969) we found no specific differences in the ciliary sorting mechanisms and concluded that the specific differentiation in the size of particles accepted was based on

the quality or quantity of the mucus secreted, although there may be differences in the ciliary sorting mechanisms of the Tellinacea as a whole.

2. The inclusion of the enzymatic characteristic in the sand grain feeders is justified on the basis of *Macoma secta* (Conrad, 1837) only, and it would be most interesting to see if this applies in the cases of the other sand grain eaters in the Tellinacea. It is postulated that the proteases particularly aid in the release of the colonies of microorganisms from the surfaces of the sand grains.

3. The large extension of the gastric shield is found in many of the other Tellinaceans (Yonge, 1949).

The use of any single criterion as a basis for feeding types is open to the kind of criticism put forward by Morton (1960), and reported by Pohlo (1969): "the difference in feeding habits is not great, for surface deposits are stirred into suspension and deposit feeders imbibe suspended material." However, by considering all the factors concerned in feeding there emerge three types. Two of these types are the suspension feeders and the fine deposit feeders. The main distinction between them is that the gastric contents of the former are composed of phytoplankton during those months when it is available. The other distinctions, such as size of particles accepted, and mucus quality, are more matters of degree. However, all warrant the division into two categories. The third type "sand grain eaters" is distinctive in all respects.

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